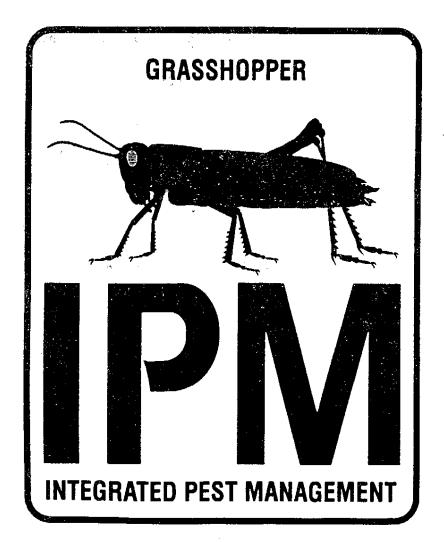
COOPERATIVE GRASSHOPPER INTEGRATED PEST MANAGEMENT PROJECT

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GRASSHOPPER CONTROL: IMPLICATIONS OF INVESTIGATIONS INTO POPULATION/COMMUNITY ECOLOGY

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Introduction:

During 1992, two objectives were addressed: 1) could a previously proposed population model (Belovsky 1992) be experimentally validated so that pest managers could be confident of its predictions for the design of control strategies? 2) could the model's parameters and predictions be simplified and made operational so OICs could employ it in implementing grasshopper control in a timely and economical fashion? These objectives, rather than generating new concepts, address GHIPM's technology transfer mission by translating scientific findings into a form that can define better control and monitoring strategies. For example, it may be possible to integrate existing population processes with reduced pesticide application to prevent grasshopper populations from attaining densities that cause economic damage.

My grasshopper population/community ecology studies supported by GHIPM have indicated a shifting importance of density independent abiotic-induced mortality, food limitation, interspecific competition, parasitism and predation in determining grasshopper abundances in different habitats and years (Belovsky 1986a, b, 1990a, 1990b, 1991, 1992, in press, Belovsky and Slade in press a, b, submitted, Belovsky et al. 1990, Lietti de Guibert et al. submitted). These processes have been integrated into a population model (Belovsky 1992). The model indicates that grasshopper populations that cause economic damage are food-limited, either chronically or periodically, and it may be possible for pest managers to shift populations into a natural enemy- and abiotic mortality-limited state, where economic damage is less likely, through limited control efforts.

Materials and Methods:

Only new methods developed will be presented. However, previous methods for the study of predation, competition and food abundance were also employed (Belovsky 1990).

- 1) Validation of the population model's implications for control/monitoring strategies. Populations of *Melanoplus sanguinipes* were studied in enclosures constructed over natural vegetation at the National Bison Range, Montana. The enclosures enclosed 9m² (3m X 3m) of natural vegetation and were constructed in the following manner:
 - a) vinyl garden edging was buried 10 12cm in the soil;
 - b) six 45 cm steel stakes were driven 30 cm into the soil at the enclosure's corners and at the middle of opposite sides;
 - c) a frame composed of 3 sections of aluminum pipe (4m long) was constructed by bending each section into a U-shape and the sections were supported by inserting the ends over opposite pairs of stakes, so the frame stood 50cm above the soil and spanned 3m;

- d) a tent sewn from insect screen covered the frame, and it contained 2 sleeves on opposite sides, permitting access to the enclosure that could be closed with drawstring;
- e) the tent was fastened to the garden edging using vinyl clips.

Enclosures were constructed in a habitat with a simple plant community (2 grasses: Poa pratensis, Elymus smithii; 1 forb: Heterotheca villosa); grasses comprised >95% of biomass (dry mass). A simple habitat makes food abundance measurements easier to make. The enclosures were placed in a 3 X 4 grid, separated by 2m. This was accomplished by June 20, 1992. Four treatments with 3 replicates were employed and randomly assigned to exclosures:

- i) controls M. sanguinipes populations started at the average density observed at the site on June 20;
- ii) decreased density populations started at 50% of the average density observed at the site on June 20;
- iii) increased density populations started at 125% of the average density observed at the site on June 20;
- iv) control density with supplemental food food supplemented by providing water every 2 days, so that an additional 3.5 cm of water/month (June 20 Sept. 1) was available.

The grasshoppers in the enclosures and outside were censused weekly (June 20 - Sept. 15). Each enclosure contained 60.10m^2 rings that were randomly placed when the enclosures were constructed, while 16 rings were randomly placed outside the enclosures. Censusing was conducted by 3 observers. For the enclosures, 2 individuals knelt on either side of a ring, looking through the screen, while the third individual poked the vegetation in the ring with a pole placed through the tent's sleeves. For the outside area, a ring was observed from a distance of 2m, while the vegetation within it was poked with a pole. On each census-day, the rings were counted 3 times (9AM, 2PM, 7PM). Based upon the initial censuses of M. sanguinipes nymphs in each enclosure and outside area, treatment densities were attained by adding or removing nymphs to attain the desired density relative to the outside average. Other grasshopper species were removed at the start and during the experiment when observed; this, however, was not a problem since they comprised < 20% of the total numbers.

Enclosures prevented normal predation by birds and mammals, while spider predation still occurred. Therefore, to maintain natural predation by vertebrates, previous studies (Belovsky et al. 1990) relating predation rates to grasshopper density, were employed with each week's census to determine how many grasshoppers should be removed from the enclosure. These were removed the day before the following week's census, using an insect net placed through the tent's sleeve. Grasshoppers that were caught were kept for later analysis (males and nymphs were placed in 70% ethyl alcohol, while females were frozen).

The treatment densities were selected, given the grasshopper population model (Belovsky 1992), hypothesizing that:

- a) the lower densities should indicate natural enemy- and abiotic mortality limitation;
- b) the increased density should indicate food-limitation;
- c) the control density could indicate either of the above possibilities with supplemental food having:
 - i) no effect, if the control densities were limited by natural predators and abiotic mortality;

ii increased density, if the control densities were limited by food. Five 0.1 m² cages like those previously employed were placed in the area and stocked with 10 *M. sanguinipes* nymphs on June 20 to determine densities in the absence of predation and with large initial densities. These populations should reflect food-limitation. Three 100 m² avian exclosures and controls like those previously employed provided an independent assessment of whether avian predation reduced densities. The use of previously employed methods provide comparison with the exclosure densities to examine for possible experimental inconsistencies. At the end of the experiment (Sept. 15):

- a) the remaining grasshoppers in the enclosures were caught (males were preserved in 70% ethyl alcohol and females were frozen to permit later counts of *corpora lutea*);
- b) the vegetation in 6 0.05m² plots in each enclosure was clipped, sorted between grasses and forbs, dried, weighed to measure biomass, ground and chemically digested (HCl and pepsin, Belovsky 1990a), as an index of plant digestibility to the grasshoppers;
- c) 25 randomly chosen blades of grass in each exclosure were examined for feeding by grasshoppers;
- d) reproduction by these populations will be measured as the emergence of nymphs by censusing within the enclosures during June, 1993.

The experiment will be repeated in 1993-1994 in a different vegetation type.

2) Technology transfer - translating the model into a form usable by OICs to better plan grasshopper control. The model is not readily adapted to the development of pest control/monitoring strategies, since the parameters require detailed measurements and the model's solution can be difficult (Belovsky 1992). Therefore, parameter simplifications are necessary, as well as the development of general conditions that lead to food-limitation (economic damage) versus natural enemy- and abiotic mortality-limitation (non-economic damage). This must be accomplished before OICs can use the insights provided by the model to assess the potential for modifying grasshopper populations to reduce the potential for economic damage and the necessary intensity of control efforts.

The simplifications required to accomplish this technology transfer are being addressed in two ways. First, given the range of values observed in my studies and other studies reported in the literature for the model's parameters, the importance of each parameter must be assessed through sensitivity analysis. The ability of the more important parameters to identify populations that can and cannot cause economic damage can be determined using Discriminant Analysis. Second, because many of these specific parameters may be too difficult for OICs to measure for the populations that they are responsible for monitoring and controlling, surrogate measures that OICs already have available or could easily obtain need to be correlated with the model parameters. This makes the model and its predictions operational.

Results:

1) Validation of the population model's implications for control/monitoring strategies.

a) In the same habitat, natural enemy and abiotic-induced mortality could limit grasshopper populations in enclosures that started with low numbers of nymphs, while food-limitation could be observed with higher initial abundances of nymphs (Fig. 1). This result indicates that grasshopper population dynamics during a year are determined by the initial numbers of nymphs emerging in relation to the food resource. Therefore, under identical

food abundances and environmental conditions, a population can attain the alternate states of natural enemy- and abiotic mortality-limitation or food-limitation depending upon initial numbers. Furthermore, this implies that populations that cause economic damage (i.e. food-limited) might be shifted into a state where economic damage will not occur (i.e., natural enemyand abiotic mortality-limited) through moderate reductions of nymphal abundances.

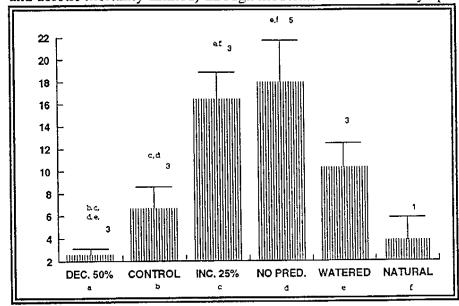


Figure 1. Adult grasshopper densities (± SE) observed from Aug. 2 through Sept. 15 in the treatments. The numbers for each treatment reflect the replicates. Statistical comparisons are based upon repeated measure ANOVAs (6 censuses during the period) and statistical differences (P ≤ 0.05) are represented by the letters.

b) Food-limited grasshopper populations imposed considerably more damage on the vegetation than the natural enemy- and abiotic mortality-limited populations (65.7 \pm 13.4% vs. 33.3 \pm 8.94%, t = 5.25, df = 13, P \leq 0.001). These results indicate that simply shifting populations from one state to the other through a moderate reduction in nymphal abundance could reduce damage to the vegetation by as much as 50%. Therefore, major reductions in the economic damage by grasshoppers can be attained with moderate control efforts (see below).

c) Initial densities in the enclosures required to produce food-limited populations can be determined using piece-wise linear regression (Fig. 2). This analysis

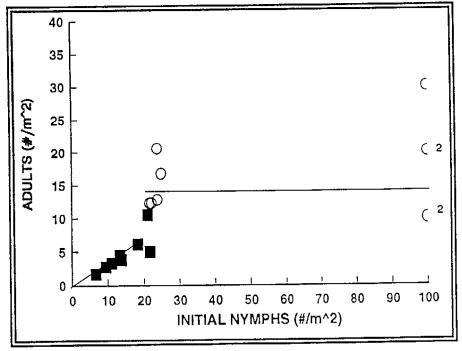


Figure 2. The initial density determines the population' constant density from August 2 through September 15 when natural enemyand abiotic mortality limits populations, but when food is limiting, initial density is not important. In this respect, piece-wise linear regression can distinguish between these alternative states.

indicates that for the abiotic conditions (39% density independent mortality) and food abundance (food-based carrying capacity = 14.3 adults/m²) occurring at the study site, initial densities are good predictors of which of the two population states will emerge ($r^2 = 0.83$, df = 13, $P \le 0.01$). Since the natural populations were observed to be natural enemy- and abiotic mortality-limited, initial nymphal densities would only have had to increase by 20% (16.7 vs. 13.8 nymphs/m²) to produce food-limited populations. Therefore, the differences in initial densities needed to produce populations causing economic damage and the degree of control necessary to prevent damage can be very small, e.g., an 18% lower density can reduce damage to vegetation by 50%.

- 2) Technology transfer translating the model into a form usable by OICs to better plan grasshopper control. Two levels of sensitivity analysis with the population model (Belovsky 1992) have been addressed and interpreted in light of information available to OICs:
- a) Environmental conditions necessary to produce populations that can cause economic damage (food-limited). Using ranges of parameter values expected from my studies and the literature, the model was solved to determine whether or not the population could produce economic damage (i.e., attain food-limitation). The model's solutions were then categorized as always causing damage, periodically causing damage, and never causing damage. The parameter values and the category produced were then analyzed using Discriminant Analysis to assess which parameter values predicted the categories best. Discriminant Analysis indicated that the model's complete set of 6 parameters explained the populations' categories correctly 93% of the time. However, 2 parameters (food abundance and abiotic mortality) alone could correctly identify categories 83% of the time. Therefore, these two parameters should be sufficient for OICs to assess a population's potential to cause damage (Fig. 3), and the validation experiments described above will test this expectation.

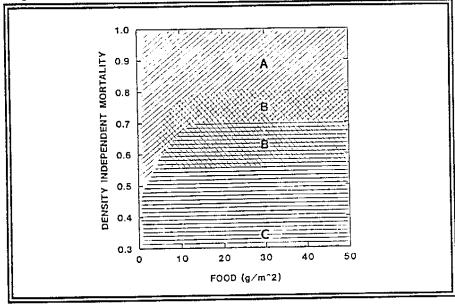


Figure 3. The 3 categories (A = natural enemy/abiotic-limitation; B = periodic food-limitation; C = consistent food limitation) defining the potential for populations to cause economic damage are presented as a function of 2 of the model's parameters: food abundance and abiotic mortality.

b) Whether or not a population that can cause economic damage will do so, and the minimum degree that a population needs to be reduced to prevent damage depends upon a threshold for initial density and the observed initial density (see Validation). From the model, the threshold initial density (T) above which damage will occur (food-limitation) should be a linear function:

T = a + Food/(1 - abiotic mortality - b) - c/(1 - abiotic mortality - b),

where a, b and c are constants. Therefore, T is expected to increase with food abundance and abiotic mortality, but additional data from the enclosure experiments will be required from the same site in other years and from other sites before a regression for T can be developed, since at present only a single estimate of T, food abundance and abiotic mortality are available.

c) Information available to OICs that can be used to assess food abundance, abiotic mortality, and initial density. With the current level of remote sensing technology for assessing plant biomass or regressions relating annual weather parameters (precipitation and air temperature) with plant biomass, adequate estimates of food abundance should be available. Abiotic mortality should also be a function of weather conditions. Initial density is a parameter commonly monitored by OICs. Therefore, with the above-developed relationships and this information, OICs should be able to apply the model to assess which populations can cause economic damage, and the minimum level of control needed to prevent damage.

Discussion:

From the above validation results, it is apparent that initial population density is an important parameter that OICs need to monitor in order to design control programs. This is not a new realization; however, the technology transfer of the population model (Belovsky 1992) indicates 4 important new considerations:

- 1) The threshold for initial population density that discriminates between the population becoming natural enemy- and abiotic mortality-limited (no economic damage) vs. food-limited (economic damage) varies with plant productivity in the environment (food abundance) and intensity of abiotic mortality (weather).
- 2) Certain environmental conditions (food abundance and weather) can prevent populations from causing economic damage (i.e., regardless of initial density they will always be natural enemy- and abiotic mortality-limited). These populations are not of concern to OICs, and can be identified and eliminated from monitoring efforts.
- 3) Certain environmental conditions will periodically or chronically produce populations that cause economic damage. These populations are of concern to OICs, and can be identified for control purposes.
- 4) Control measures that dramatically reduce economic damage do not have to result in major reductions in grasshopper densities (e.g., an 18% reduction in nymphal abundance was observed to reduce plant damage by 50%), rather the population simply needs to be forced from a state of food-limitation into a state of natural enemy- and abiotic mortality-limitation. This requires that initial densities be reduced below a threshold value. Therefore, an OIC can customize control measures (e.g., how intensive an approach is needed), if initial density is known along with the density threshold.

Summary:

- One goal of GHIPM is to identify alternative control methods and more specific levels of application needed to prevent economic damage.
- A grasshopper population model based upon experimentally examined ecological mechanisms defines environmental conditions that produce populations that cause economic damage, and the intensity of control (% mortality) needed to prevent damage.
- Control intensity is defined as a level of mortality needed to shift the population into a state where natural enemy and abiotic mortality prevent economic damage; therefore, control methods and levels can be specified to supplement natural population processes.

- The specific information required by the model is being framed to take advantage of information currently available to OICs, and with the expected ranges of values, OICs can be provided with straightforward "rules of thumb" to determine whether or not a population poses an economic threat and the intensity of control needed to prevent economic damage.
- These findings are not only being developed into a set of "rules of thumb" for OICs, but also in collaboration with Berry, Kemp and Onsager at the Bozeman, ARS lab and Joern at the U. of Nebraska, a "next generation" computer model that will be more specific than Hopper is being developed.

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